Do Field Margins Enrich the Diet of the Eurasian Skylark *Alauda arvensis* on Intensive Farmland?

Author(s): Henk Jan Ottens, Marije W. Kuiper, Heiner Flinks, Jasper van Ruijven, Henk Siepel, Ben J. Koks, Frank Berendse & Geert R. de Snoo
Source: Ardea, 102(2):161-174.
Published By: Netherlands Ornithologists' Union
https://doi.org/10.5253/arde.v102i2.a6
URL: http://www.bioone.org/doi/full/10.5253/arde.v102i2.a6

Do field margins enrich the diet of the Eurasian Skylark *Alauda arvensis* on intensive farmland?

Henk Jan Ottens[1], Marije W. Kuiper[2,*], Heiner Flinks[3], Jasper van Ruijven[2], Henk Siepel[2,4], Ben J. Koks[1], Frank Berendse[2] & Geert R. de Snoo[5]

Ottens H.J., Kuiper M.W., Flinks H., van Ruijven J., Siepel H., Koks B.J., Berendse F. & de Snoo G.R. 2014. Do field margins enrich the diet of the Eurasian Skylark *Alauda arvensis* on intensive farmland? Ardea 102: 161–171. doi:10.5253/arde.v102i2.a6

To help restore food availability for birds, arable field margins (extensively managed strips of land sown with grasses and forbs) have been established on European farmland. In this study we describe the effect of field margins on the diet of Eurasian Skylark nestlings and adults living on intensively managed Dutch farmland. We tested the hypotheses that field margins offer a higher diversity of invertebrate prey than intensively managed crops, and that the diet of nestlings receiving food from field margins will therefore be more diverse than that of other nestlings. Field margins had a greater variety of invertebrate prey groups to offer than the intensively managed crops. Coleoptera were the most frequently and most abundantly eaten prey group by both adults and nestlings. Together, Coleoptera, Diptera, Lepidoptera, Hymenoptera and Araneae accounted for 91% of the nestling diet. Nestlings ate larger prey items and a larger proportion of larvae than adults. Almost 75% of both adults and nestlings consumed plant material, perhaps indicating a scarcity of invertebrate resources. When provided with food from field margins, the mean number of invertebrate orders in the nestling diet increased significantly from 4.7 to 5.5 and the number of families from 4.2 to 5.8 per sample. Thus, birds that used field margins for foraging could indeed provide their young with more invertebrate prey groups than birds only foraging in crops and grassland.

Key words: agri-environmental management, birds, conservation, diet, diversity, food availability, invertebrates

[1]Dutch Montagu's Harrier Foundation, P.O. Box 46, 9679 ZG Scheemda, The Netherlands; [2]Nature Conservation and Plant Ecology Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands; [3]Am Kuhm 19, 46325 Borken, Germany; [4]Department of Animal ecology and Ecophysiology, IWWR, Radboud University, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands; [5]Institute of Environmental Sciences, Leiden University, P.O. Box 9518, 2300 RA Leiden, The Netherlands;
*corresponding author (marije.kuiper@yahoo.com)

The Europe-wide decline of farmland bird populations during the last quarter of the 20th century can to a large degree be linked to the intensification and industrialisation of agriculture (e.g. Chamberlain *et al.* 2000, Donald *et al.* 2001a, Benton *et al.* 2003, Newton 2004, Stoate *et al.* 2009, Geiger *et al.* 2010). Major agricultural changes include increased agro-chemical inputs, land consolidation and the associated removal of natural landscape elements, improved drainage, the conversion of species-rich meadows to high-input grassland, a switch from spring to autumn sown cereals and reduced crop diversity at the landscape level. These changes have resulted in a loss of foraging habitat for farmland birds, as well as an overall reduction in the availability of invertebrate and plant food in the agricultural landscape (Wilson *et al.* 1999, Taylor *et al.* 2006, Butler *et al.* 2007, Siriwardena *et al.* 2008). To counteract the negative effects of agricultural change on food availability, agri-environmental measures such as field margins, set-asides and winter food patches have been established to restore resources (Vickery *et al.* 2002, Siriwardena *et al.* 2008, Vickery *et al.* 2009).

Various bird species prefer these semi-natural elements for foraging over cropped land, demonstrating their value as foraging habitat (Perkins *et al.* 2002, Siriwardena *et al.* 2007, Kuiper *et al.* 2013).

Presumably, the attractiveness of semi-natural habitat to birds is largely explained by higher food abundance (Vickery *et al.* 2002). However, food diversity or the availability of particular food items may also be a factor. Animals forage to regulate the intake of multiple nutrients, rather than solely maximising their energy intake (Simpson *et al.* 2004). To ensure the provisioning of all necessary nutrients, passerines feed their young a range of different prey groups (Tinbergen 1981, Krebs 1984). In particular, during the developmental stage the diet quality of birds can have profound effects on their growth, immune functioning and overall health that can extend into the adult stage (Boag 1987, Birkhead *et al.* 1999). Nutritional deficiencies can occur when prey items are absent that provide essential nutrients or amino acids, leading to reduced growth rates and later fledging (Johnston 1993, Graveland 1996, Ramsay & Houston 2003, Sillanpää *et al.* 2010).

The decrease in the overall diversity of plants and invertebrates in agricultural areas (Wilson *et al.* 1999, Vickery *et al.* 2001, de Snoo *et al.* 2012) is likely to be reflected in the diet of farmland birds. The establishment of agri-environment schemes that increase the area of un-cropped land may help to offer birds a wider variety of prey taxa in impoverished agricultural landscapes. In this paper we study the effect of extensively managed field margins on the diet of the Eurasian Skylark *Alauda arvensis*, a bird species that has been severely declining in most Western European countries (EBCC 2013). It has been shown previously that the body condition of Skylark nestlings is negatively affected when they are provided a less diverse diet (Donald *et al.* 2001b). Changes in nestling diet composition, imposed by experimentally handicapping provisioning parents, contributed to lower immune functioning and reduced long-term survival of Skylark nestlings (Hegemann *et al.* 2013). Although a scarcity of safe nesting habitat in agricultural landscapes has been identified as a major bottleneck for this species (Wilson *et al.* 1997, Chamberlain *et al.* 1999, Chamberlain & Vickery 2000, Kragten *et al.* 2008), reduced food availability and diversity may have contributed to population declines (Donald *et al.* 2001b, Geiger *et al.* 2014, Hallmann *et al.* 2014).

This paper has three objectives: (1) to compare the taxon richness of invertebrate prey groups in field margins with common crops, pasture and road verges, (2) to describe the diet of nestling and adult Skylarks on intensively managed farmland during the breeding season and (3) to assess whether field margins as a supplementary foraging habitat affect the diversity and composition of the nestling diet. We hypothesise that field margins contain a wider range of prey groups than crops and pasture. Consequently, the diet of nestlings receiving food from field margins is expected to be more diverse than the diet of nestlings where parents have no access to field margins.

METHODS

The study was carried out from April to August 2011 and 2012 in the province of Groningen in the northeast of The Netherlands. The research area of approximately 970 ha was situated on marine clay and agriculture was the main land use. The predominant crops were winter wheat (±50%), silage grassland (±25%), maize (±8%), lucerne (±5%), sugar beet (±5%) and rapeseed (±3%). In this province, field margins are one of two possible agri-environmental prescriptions for breeding birds on arable land, the other being set-aside. Field margins account for 92% of the total area of field margins and set-aside together (Wiersma *et al.* 2014). The surface area of field margins was approximately 5% of the cropped land in both years. Field margins generally were 12 m wide and 500–1000 m long, sown with a mixture of grasses, forbs and cereals (Figure 1). The age of the field margins ranged between one and twelve years. Regulations required that 20–70% of the field margin surface was cut twice-annually to keep the vegetation open; once between 1 March and 15 April and once between 15 July and 15 September.

Invertebrate sampling

Invertebrates were sampled in 2011 and 2012 to compare prey taxon richness between field margins, crops, grassland and verges (strips of grassy vegetation along roads and ditches) using a modified leaf vacuum (McCulloch MAC GBV 345) with a 12 cm diameter suction tube. Sampled crops were winter wheat (intensively managed), lucerne (cut two or three times per year followed by manure application, no pesticide use) and grassland (high-input silage fields cut five times per year). Each suction sample consisted of five subsamples of 15-seconds vacuum sessions within a bottomless circular frame (50 cm diameter), thus sampling a total area of 0.982 m^2 per sample. Five field margins were sampled in both years. Two verges were sampled in 2011 and four in 2012. Of each crop type

Figure 1. Field margin with grasses, forbs and cereals in the first year after sowing. Ganzedijk, The Netherlands, July 2010.

(grassland, lucerne and wheat) two fields were sampled in 2011 and five in 2012. Each margin, verge and field was sampled five times throughout the breeding season, from mid-May through mid-July. Sampling was conducted in sunny and dry weather conditions only. Invertebrate numbers were converted to dry biomass by applying the length-biomass relationships given in Hawkins *et al.* (1997, Stylommatophora), Ganihar (1997, Isopoda) and Sage (1982, all other taxa).

Diet

Skylark nests were located as part of a study monitoring reproductive success and the effect of field margins on breeding and foraging. Foraging habitat use by parental birds was recorded during two one-hour observations on two separate days, observed from a hide using binoculars (see Kuiper *et al.* 2013 for detailed methods). 95 faecal droppings were collected from 50 broods in 2011 and 16 broods in 2012, with nestlings aged between 5 and 8 days. Samples were collected between 26 April and 6 August, with 70% of the samples being collected in June and July. Nestlings usually defecated when they were handled for weighing and ringing, after which faecal samples were stored in vials with sodium chloride for preservation. Mostly two but sometimes one or three faecal droppings were collected per brood. Samples from nine adult birds were collected when they were caught in mist nets that were placed over the nest for the purpose of placing radio tags for a different study (Ottens *et al.* 2013).

For examination, the faeces were soaked in water for 30 min and analysed under a binocular microscope at 20× magnification using a standard method (Ralph *et al.* 1985, Flinks & Pfeifer 1987). Prey fragments were identified to class, order and where possible to family, genus or species level. Field guides, taxonomic keys and reference material were used to aid identification. Because of uncertainties in taxonomy or identification, the subclass Acarina and clade Stylommatophora were used as taxonomic entities equivalent to order, and the superfamily Aphidoidea and suborders Heteroptera and Auchenorrhyncha were used as equivalents to family. Based on the animal remains, the minimum number of individuals per taxon was assessed. Invertebrate length was estimated using a reference collection and information from the literature (Calver & Wooller 1982, Ralph *et al.* 1985, Flinks & Pfeifer 1987). Diet diversity was calculated as the total number of unique invertebrate

taxa present per dropping. The number of prey taxa was used as a measure of diversity rather than a diversity index that incorporates evenness, because studies on this subject indicate that equal amounts of each prey taxon are not necessary to balance nutrient intake (Westoby 1978, Tinbergen 1981, Simpson *et al.* 2004).

The method of faecal analysis to study the diet of birds causes less disturbance than invasive methods such as neck-collars and allows for a better determination of food items than observation by telescope or camera. Concerns have been raised about the differential digestion of prey items, which could yield inexact estimations of the proportions of different prey groups (Moreby & Stoate 2000), but in a comparative study with Skylark nestlings, no differences in diet composition were detected between faecal analysis and applying neck collars, possibly because the passage of food through the gut is relatively quick in Skylark nestlings (Poulsen 1995).

Data analyses

Differences in invertebrate diversity between habitat types were analysed using a Generalised Linear Mixed Model with unstructured covariance structure. The number of taxa identified after suction sampling was entered as the dependent variable with Poisson distribution and identity link (taxa included Araneae, Auchenorrhyncha, Chilopoda, Coleoptera, Diplopoda, Diptera, Heteroptera, Hymenoptera, Isopoda, Lepidoptera imagoes, Lepidoptera and Symphyta larvae, Opiliones, Orthoptera and Stylommatophora). Sampling site was entered as subject and catch round as the repeated factor, so that each catch round in the same margin or field was considered a repeated observation. Habitat type and catch round were added to the model as fixed factors and the interaction between habitat type and catch round was entered to detect whether differences in prey diversity changed over time. To account for possible differences between years, year was added as a random factor. When differences were significant, pairwise post-hoc tests were conducted with Bonferroni-correction.

To characterise the diet in more detail, the length of consumed invertebrate prey items was compared between nestlings and adults using a General Linear Mixed Model. The length of the prey items was log-transformed to achieve normality of residuals and entered as the dependent variable. Nest and adult bird identity were entered as random factor, so that each prey item eaten by the same brood or adult bird was regarded as a repeated observation. The life stage of the subjects (nestling or adult) was entered as an explanatory factor. Year was added as a factor to control for possible differences in prey size between years.

To assess the effect of foraging in field margins on the diversity of the nestling diet, Generalised Linear Mixed Models were used. The number of invertebrate orders or families in the diet per dropping was entered as the dependent variable with Poisson distribution and identity link. Nest identity was entered as the subject and dropping as the repeated factor, so that each dropping collected from the same brood was considered a repeated observation. The use of field margins as a foraging habitat by parents during the foraging observations was entered as a factor. To test for possible changes in diet diversity over the course of the breeding season, sampling date was added as a covariate. Sampling date was also tested in a quadratic relationship with diet diversity, but this did not provide a better fit to the data and only the linear term was used in the final models. Year was added as a random factor to control for possible differences in prey diversity between years. Only nests where foraging observations had been conducted were included in this analysis (53 nests, of which 20 had been fed from field margins). Chi-square tests of independence were used to test whether the frequency of occurrence of invertebrate orders and families in the diet differed between nestlings fed from field margins and those not fed from field margins. The Benjamini–Hochberg correction was applied to reduce the chance of false positives when performing multiple tests (Benjamini & Hochberg 1995, Waite & Campbell 2006).

All statistical analyses were performed with SPSS v.21 (IBM, Armonk, New York). Means are given with standard errors.

RESULTS

Available prey

Summed over all habitat types, Diptera (true flies), Coleoptera (beetles) and Araneae (spiders) were the most abundant prey groups sampled by suction sampling (Figure 2). Also Isopoda (woodlice), Stylommatophora (snails and slugs), Auchenorrhyncha (cicadas) and Heteroptera (bugs) were relatively common. Opiliones (harvestmen), Lepidoptera (moths and butterflies), Hymenoptera (ants and sawflies) and Orthoptera (grasshoppers and crickets) were found in small quantities.

The taxon richness of invertebrate prey differed significantly between the sampled habitat types ($F_{4,32} = 25.7$, $P < 0.001$) and between the five catch

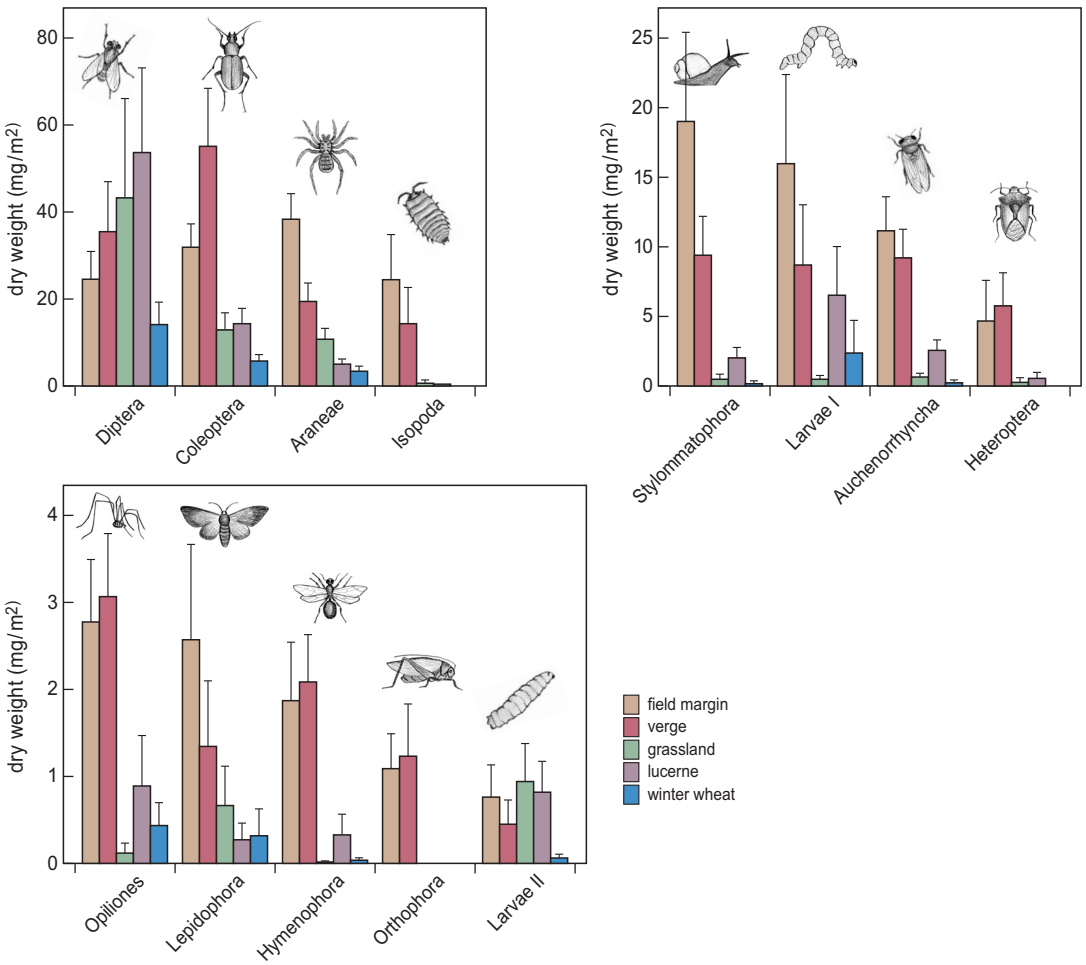

Figure 2. Biomass contributions of invertebrate groups in five different habitat types, averaged over the breeding seasons of 2011 and 2012 (+SE). Note the variable scale of the y-axes. Larvae I include Lepidoptera and Symphyta larvae, Larvae II include Diptera and Coleoptera larvae.

rounds ($F_{4,32} = 9.3$, $P < 0.001$). In addition, the differences in invertebrate diversity between habitat types changed over time (interaction between habitat type and catch round: $F_{16,32} = 1.9$, $P < 0.05$). Field margins contained more invertebrate taxa than winter wheat throughout the entire sampling period, more than grassland during both catch rounds in June, and more than lucerne in the end of June. There were no differences between field margins and road verges. Averaged over the whole sampling period, the mean number of taxa was 5.4 ± 0.3 in field margins, 6.0 ± 0.4 in road verges, 3.9 ± 0.3 in lucerne, 2.9 ± 0.3 in grassland and 2.1 ± 0.2 in winter wheat.

All invertebrate taxa, with the exception of Diptera and larvae of Diptera and Coleoptera, were found in higher quantities in field margins and verges than in grassland, lucerne and winter wheat (Figure 2). Certain taxa were found almost exclusively in field margins and verges, such as Isopoda, Orthoptera, Hymenoptera, Stylommatophora, Heteroptera, Auchenorrhyncha and Opiliones.

Diet composition

In the diet of 66 broods, 1619 invertebrate prey items were recognised, of which 1611 could be identified to at least order level (see Table A1 for a detailed overview). In the faeces of nine adult birds, remains of 68 prey items were found that could all be identified to at least order level (Table A2). Some prey orders, including Stylommatophora, Isopoda and Lepidoptera, could never be identified to family level and are thus underrepresented in analyses of family diversity.

Coleoptera were the most important prey group for nestlings as well as adult birds. 94% of all broods and

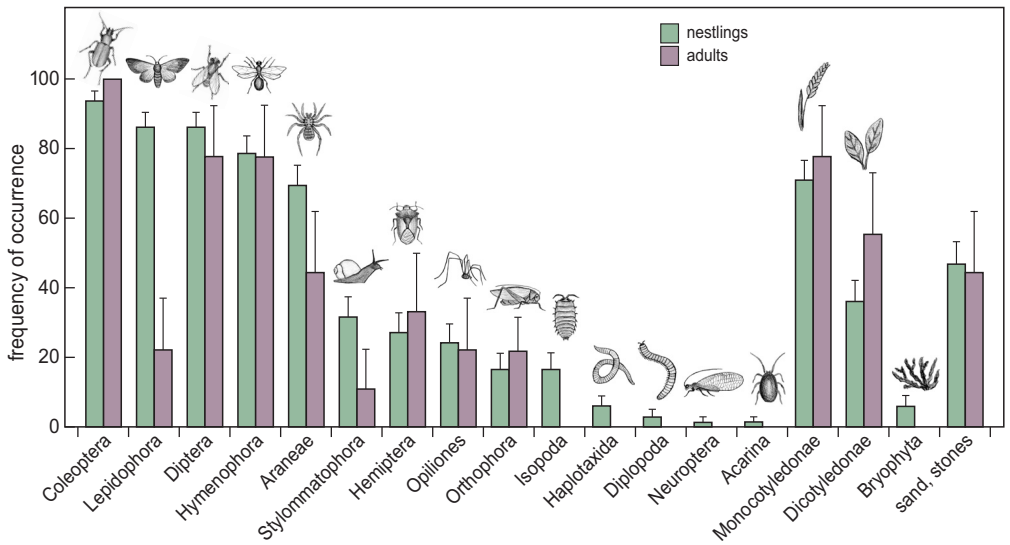

Figure 3. Frequency of occurrence of different invertebrate and plant groups in the diet of 66 Skylark broods and nine adults (+SE).

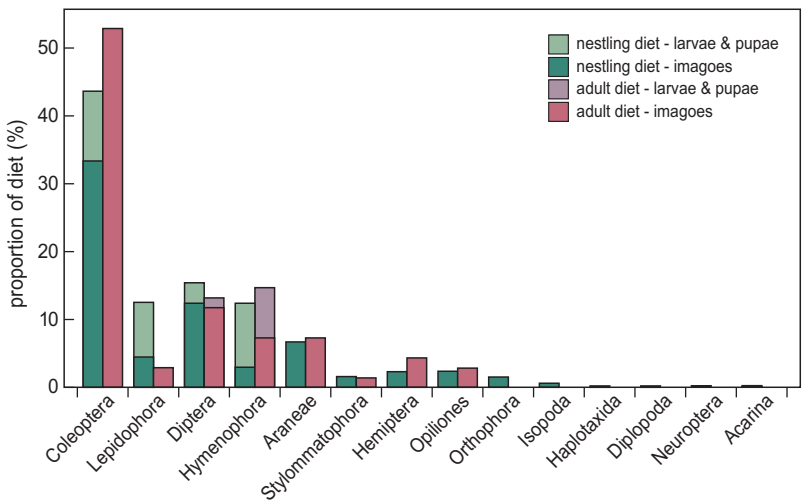

Figure 4. Proportion of invertebrate prey groups in the diet of Skylark nestlings and adults, based on prey numbers.

100% of all adults had eaten Coleoptera (Figure 3) and this group accounted for 44% and 53% of the total number of invertebrate prey items eaten by nestlings and adults, respectively (Figure 4). Eleven families of Coleoptera were identified in the diet of nestlings, of which Carabidae (62%), Elateridae (14%), Curculionidae (7%) and Byrrhidae (6%) were the most numerous (Table A1). One quarter of the Coleoptera eaten by nestlings were larvae, while adults ate imagoes only (Figure 4).

Lepidoptera, Diptera, Hymenoptera and Araneae each formed between 7–15% of the diet of nestlings and occurred in the diet of 70–86% of all broods. Adults ate fewer Lepidoptera than nestlings and only took imagoes, while nestlings received a large proportion of larvae (64%). Of the Diptera that could be identified, Tipulidae were the most abundant family (95%). Within the Hymenoptera, the Symphyta were by far the most frequently eaten family (90%), mainly pupae (60%) and larvae (33%). Within the Araneae, the families Lycosidae (75%), Linyphiidae (13%) and Salticidae (10%) were the most numerous. Minor prey groups for nestlings were Stylommatophora, Hemiptera, Opiliones, Orthoptera and Isopoda, which were eaten

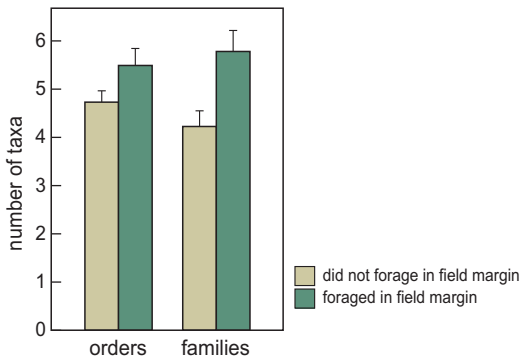

Figure 5. Mean number of invertebrate orders and families in the diet of Skylark nestlings of which the parents did or did not forage in field margins (+SE).

by 17–32% of all broods but comprised only 1–2% of the total number of prey items. Oligochaeta, Diplopoda, Neuroptera and Acarina occurred in the nestling diet sporadically. The last six groups were not found in the diet of adults.

Nestlings ate significantly larger invertebrates than adults ($F_{1,1673} = 42.9$, $P < 0.001$). The size of nestling prey ranged between 0.3 and 50 mm, with a mean of 10.7 ± 0.2 mm. The mean prey size of adult birds was 6.1 ± 0.5 mm, ranging between 1 and 16 mm. There were no differences in prey sizes between years ($F_{1,1673} = 2.6$, $P = 0.10$).

Both nestlings and adults consumed plant material (Figure 3), the vast majority being seeds and occasionally stems, leaves and inflorescences of *Triticum* and *Secale* (Tables A2, A3). Adult birds also ate other Poaceae, such as *Setaria* and *Poa annua*. Nestlings were fed a range of Dicotyledonae, including seeds of *Taraxacum officinale* (Asteraceae), *Capsella bursa-pastoris* (Brassicaceae) and *Lamium amplexicaule* (Lamiaceae). Remains of Euphorbiaceae, Caryophyllaceae, Geraniaceae, Plantaginaceae, Polygonaceae and Violaceae were also found in the diet. Adults ate seeds of Asteraceae and Polygonaceae and leaves from unidentified Dicotyledonae. Both nestlings (47%) and adults (44%) had small stones (mean length 1.3 ± 0.11 mm, predominantly gastroliths) and sand in their faeces. Two nestlings had eaten pieces of charcoal.

Diet diversity and effect of field margins

The mean number of invertebrate orders and families in the diet was significantly larger for nestlings that were fed from field margins than for other nestlings (orders: $F_{1,78} = 6.6$, $P < 0.05$; families: $F_{1,78} = 8.8$, $P < 0.01$; Figure 5). The diversity of invertebrate families in the diet decreased significantly over the course of the breeding season ($F_{1,78} = 9.1$, $P < 0.01$), while the diversity of invertebrate orders remained stable ($F_{1,78} = 0.2$, $P = 0.7$).

When comparing the frequency of occurrence of invertebrate taxa in the diet (Figures 6, 7), the diet of broods that received food from field margins contained higher frequencies of the order Opiliones ($\chi^2_1 = 4.2$, $P = 0.042$), the Dipteran family Tipulidae ($\chi^2_1 = 8.3$, $P = 0.004$) and the Coleopteran families Elateridae ($\chi^2_1 = 6.3$, $P = 0.012$), Byrrhidae ($\chi^2_1 = 6.1$, $P = 0.013$) and Curculionidae ($\chi^2_1 = 4.1$, $P = 0.044$), but the differences did not remain significant after applying the Benjamini–Hochberg correction for multiple testing.

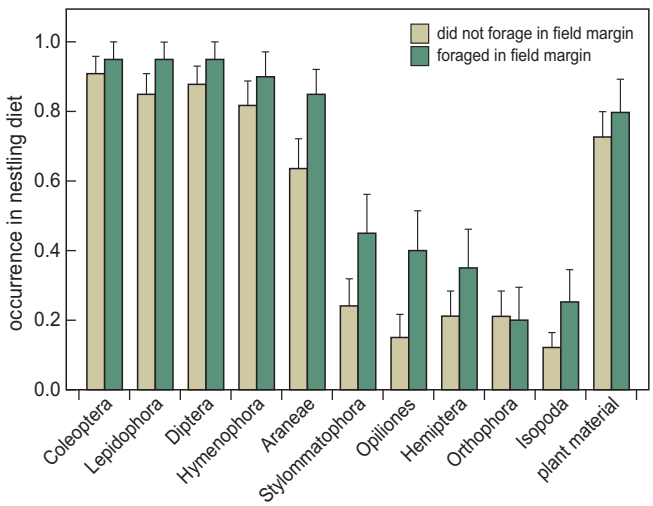

Figure 6. Frequency of occurrence of different invertebrate orders in the diet of Skylark nestlings of which the parents did or did not forage in field margins (+SE).

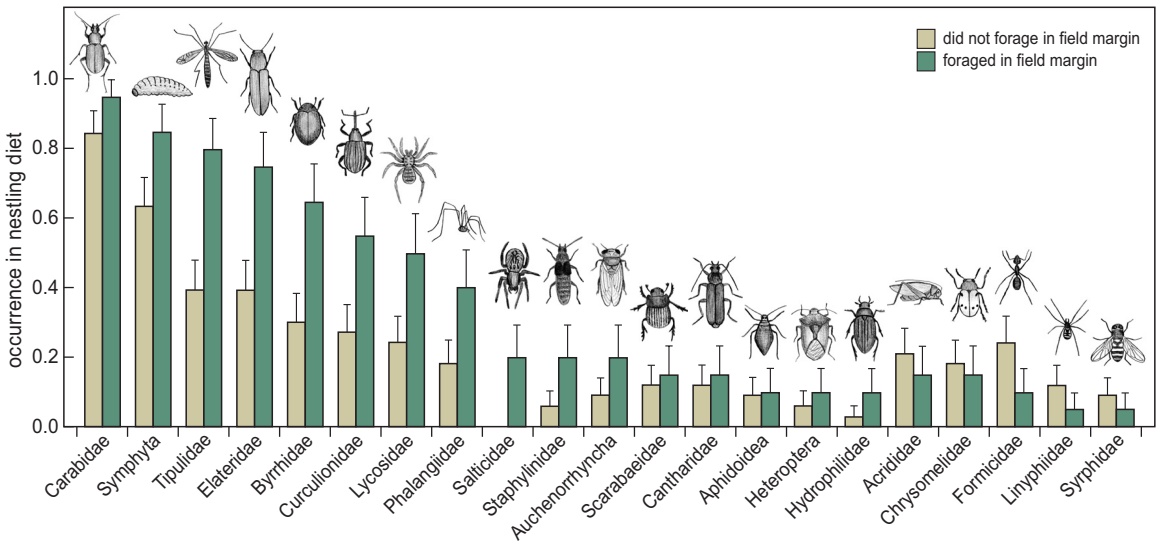

Figure 7. Frequency of occurrence of different invertebrate families in the diet of Skylark nestlings of which the parents did or did not forage in field margins (+SE).

DISCUSSION

The diet composition of Eurasian Skylarks in the north of The Netherlands appeared to be broadly comparable with other parts of Europe in terms of the range of prey groups eaten, although differences exist in the relative abundances of groups (Jenny 1990, Poulsen & Aebischer 1995, Donald *et al.* 2001b, Smith *et al.* 2009). Coleoptera were the most numerous prey item, which is similar to some earlier studies (Donald *et al.* 2001b, Smith *et al.* 2009), although very low proportions of Coleoptera have been found elsewhere (Jenny 1990, Poulsen & Aebischer 1995). A comparison of diet composition and prey availability by Jenny (1990) indicated that Coleoptera were actively avoided, leading to the hypothesis that this prey group is less preferential because of their longer handling time and the slower digestion of hard body parts. Our findings partly contradict this hypothesis, because the consumption of Coleoptera in our study site seemed to be larger than would be expected based on Coleoptera abundance in the invertebrate samples. It is interesting to note, however, that a considerable proportion of the Coleoptera provided to the nestlings were larvae, which do not require the removal of elytra, so that their handling time is reduced compared to imagoes (Poulsen & Aebischer 1995). Additionally, Coleoptera larvae may be preferred because the consumption of insect larvae in general has been shown to improve the body condition of Skylark nestlings (Donald *et al.* 2001b).

Compared to other studies (Weibel 1999, Holland *et al.* 2006, Smith *et al.* 2009), the amount of plant material in the nestling diet was relatively large: 79% of all broods had eaten plant material and the number of plant items accounted for 18% of the total amount of food items. This could be an indication that the availability of invertebrates was insufficient. On the other hand, foraging in invertebrate-rich field margins did not decrease the abundance of plant material in the diet, so plants could also have been taken to supply certain nutrients. Skylark nestlings ate only low quantities of less preferential prey groups such as aphids and ants, which have been associated with parasitic infections and reduced growth and survival in chicks of Grey Partridge *Perdix perdix* (Borg & Toft 2000, Browne *et al.* 2006).

Although our sample size for adult Skylarks was small, the diet of nestling and adult Skylarks seemed to differ in two respects. First, nestlings ate a larger proportion of insects in the larval or pupal stage than adults, mainly of the taxa Coleoptera, Lepidoptera and Hymenoptera. Probably parents reserved insect larvae for their offspring, because this type of food is easily digested and increases the condition of nestlings (Flinks & Pfeifer 1988, Donald *et al.* 2001b). Larvae may also be fed to nestlings to supply them with sufficient water (Beintema *et al.* 1991). Second, the size of the prey items eaten by adults was much smaller than for nestlings, which could reflect a predation avoidance strategy. Reserving larger prey items for the nestlings

increases the food load that can be brought to the nest per provisioning trip, thereby reducing the number of parental visits to the nest and diminishing the chance that the nest is discovered by predators (Skutch 1949, Martin *et al.* 2000). A number of prey groups were eaten sporadically by nestlings while they were not found in the adult diet, but this was probably due to the much smaller adult sampling size.

We found that field margins contained a larger range of prey groups than regular crops and intensively managed grassland, which is in accordance with previous studies (Hassall *et al.* 1992, Frank 1997, 1999, Denys & Tscharntke 2002). The diversity of prey groups in field margins was generally comparable to road and ditch verges, which are semi-natural habitat elements with a more permanent character. Foraging in field margins by Skylark parents significantly increased the number of invertebrate taxa in the nestling diet, both at order and family level. Comparisons of the frequency of occurrence of the taxa in the diet indicated that the improved diversity was due to small but consistent increases in the frequencies of nearly all taxa, rather than specific taxa being unique for a diet collected in field margins. Contradicting our results, an earlier study found a lower number of invertebrate orders in the diet of nestlings that were brought up in a territory containing wildflower strips than in territories without such strips (Weibel 1999). It is possible that in this area, certain prey groups were present in wildflower strips that were so profitable that other taxa were taken less frequently. But also the accessibility of these strips may have played a role, because not all prey groups may have been within reach for Skylarks when the vegetation was dense or tall (Odderskær *et al.* 1997).

Considering the decline in invertebrate diversity on farmland (Wilson *et al.* 1999) and the importance of diet composition and diversity for the health and growth of birds (Westoby 1978, Tinbergen 1981, Boag 1987, Johnston 1993, Borg & Toft 2000, Donald *et al.* 2001b, Ramsay & Houston 2003), the connection between these subjects and its role in the ongoing decline in farmland birds is in clear need of further research. This study shows that field margins can supply invertebrate groups that are low in abundance in regular crops and intensively managed grassland and that Skylark parents that forage in field margins can provide their young with a more diverse diet. Further study is required to establish whether the increase in diet diversity implies that field margins also deliver a nutritionally more complete diet, and whether a more diverse diet will ultimately lead to improved growth and health of Skylark nestlings.

ACKNOWLEDGEMENTS

We are very grateful to the farmers who kindly allowed us to carry out this research on their properties and provided us with useful information and practical assistance. For assistance during field work we thank Rémar Erens. Two reviewers are thanked for their valuable comments and suggestions to improve the paper. The research was partly funded by the Foundation Chair in Nature Conservation on Farmland, the Province of Groningen and the Prins Bernhard Cultuurfonds (Paul van Hoorn Fund, Robert Persman Fund, Bruinvis Meijer Fund, Barbara Eveline Keuning Fund).

REFERENCES

Beintema A.J., Thissen J.B., Tensen D. & Visser G.H. 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31–43.

Benjamini Y. & Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. Roy. Stat. Soc. B Met. 57: 289–300.

Benton T.G., Vickery J.A. & Wilson J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18: 182–188.

Birkhead T.R., Fletcher F. & Pellatt E.J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proc. R. Soc. Lond. B 266: 385–390.

Boag P.T. 1987. Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). Auk 104: 155–166.

Borg C. & Toft S. 2000. Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. J. Appl. Ecol. 37: 557–563.

Browne S.J., Aebischer N.J., Moreby S.J. & Teague L. 2006. The diet and disease susceptibility of grey partridges *Perdix perdix* on arable farmland in East Anglia, England. Wildlife Biol. 12: 3–10.

Butler S.J., Vickery J.A. & Norris K. 2007. Farmland biodiversity and the footprint of agriculture. Science 315: 381–384.

Calver M.C. & Wooller R.D. 1982. A technique for assessing the taxa, length and dry weight and energy content of the arthropod prey of birds. Aust. Wildlife Res. 9: 293–301.

Chamberlain D. & Vickery J.A. 2000. Spatial and temporal distribution of breeding Skylarks *Alauda arvensis* in relation to crop type in periods of population increase and decrease. Ardea 88: 61–73.

Chamberlain D.E., Wilson A.M., Browne S.J. & Vickery J.A. 1999. Effects of habitat type and management on the abundance of skylarks in the breeding season. J. Appl. Ecol. 36: 856–870.

Chamberlain D.E., Fuller R.J., Bunce R.G.H., Duckworth J.C. & Shrubb M. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37: 771–788.

de Snoo G.R., Naus N., Verhulst J., Van Ruijven J. & Schaffers A.P. 2012. Long-term changes in plant diversity of grasslands under agricultural and conservation management. Appl. Veg. Sci. 15: 299–306.

Denys C. & Tscharntke T. 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia 130: 315–324.

Donald P.F., Green R.E. & Heath M.F. 2001a. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. Lond. B 268: 25–29.

Donald P.F., Muirhead L.B., Buckingham D.L., Evans A.D., Kirby W.B. & Gruar D.J. 2001b. Body condition, growth rates and diet of Skylark *Alauda arvensis* nestlings on lowland farmland. Ibis 143: 658–669.

EBCC 2013. European Bird Census Council, Pan-European Common Bird Monitoring Scheme.

Flinks H. & Pfeifer F. 1987. Nahrung adulter und nestjunger Schwarzkehlchen (*Saxicola torquata rubicola*) einer westfälischen Brutpopulation. Vogelwelt 108: 41–57.

Flinks H. & Pfeifer F. 1988. Einfluß des Nestlingsalters auf die Nahrungszusammensetzung nestjunger Schwarzkehlchen (*Saxicola torquata*). J. Ornithol. 129: 317–324.

Frank T. 1997. Species diversity of ground beetles (Carabidae) in sown weed strips and adjacent fields. Biological Agriculture & Horticulture 15: 297–307.

Frank T. 1999. Density of adult hoverflies (Dipt., Syrphidae) in sown weed strips and adjacent fields. J. Appl. Entomol. 123: 351–355.

Ganihar S.R. 1997. Biomass estimates of terrestrial arthropods based on body length. J. Bioscience. 22: 219–224.

Geiger F., Bengtsson J., Berendse F., Weisser W.W., Emmerson M., Morales M.B., Ceryngier P., Liira J., Tscharntke T., Winqvist C., Eggers S., Bommarco R., Pärt T., Bretagnolle V., Plantegenest M., Clement L.W., Dennis C., Palmer C., Oñate J.J., Guerrero I., Hawro V., Aavik T., Thies C., Flohre A., Hänke S., Fischer C., Goedhart P.W. & Inchausti P. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11: 97–105.

Geiger F., Hegemann A., Gleichman M., Flinks H., de Snoo G., Prinz S., Tieleman B.I. & Berendse F. 2014. Habitat use and diet of Skylarks (*Alauda arvensis*) wintering in an intensive agricultural landscape of the Netherlands. J. Ornithol.: 155: 507–518.

Graveland J. 1996. Avian eggshell formation in calcium-rich and calcium-poor habitats: importance of snail shells and anthropogenic calcium sources. Can. J. Zoolog. 74: 1035–1044.

Hallmann C.A., Foppen R.P., van Turnhout C.A., de Kroon H. & Jongejans E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511: 341–343.

Hassall M., Hawthorne A., Maudsley M., White P. & Cardwell C. 1992. Effects of headland management on invertebrate communities in cereal fields. Agr. Ecosyst. Environ. 40: 155–178.

Hawkins J.W., Lankester M.W., Lautenschlager R.A. & Bell F.W. 1997. Length–biomass and energy relationships of terrestrial gastropods in northern forest ecosystems. Can. J. Zoolog. 75: 501–505.

Hegemann A., Matson K.D., Flinks H. & Tieleman B.I. 2013. Offspring pay sooner, parents pay later: experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. Front. Zool. 10: 77.

Holland J.M., Hutchison M.A.S., Smith B. & Aebischer N.J. 2006. A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. Ann. Appl. Biol. 148: 49–71.

Jenny M. 1990. Nahrungsökologie der Feldlerche *Alauda arvensis* in einer intensiv genutzten Agrarlandschaft des schweizerischen Mittellandes. Ornithol. Beob. 87: 31–53.

Johnston R.D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the house martin *Delichon urbica*. Funct. Ecol. 7: 255–266.

Kragten S., Trimbos K.B. & de Snoo G.R. 2008. Breeding skylarks (*Alauda arvensis*) on organic and conventional arable farms in The Netherlands. Agr. Ecosyst. Environ. 126: 163–167.

Krebs J.R. & Avery M.I. 1984. Chick growth and prey quality in the European Bee-eater (*Merops apiaster*). Oecologia 64: 363–368.

Kuiper M.W., Ottens H.J., Cenin L., Schaffers A.P., van Ruijven J., Koks B.J., Berendse F. & de Snoo G.R. 2013. Field margins as foraging habitat for skylarks (*Alauda arvensis*) in the breeding season. Agr. Ecosyst. Environ. 170: 10–15.

Martin T.E., Scott J. & Menge C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proc. R. Soc. Lond. B 267: 2287–2293.

Moreby S.J. & Stoate C. 2000. A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. Bird Study 47: 320–331.

Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146: 579–600.

Odderskær P., Prang A., Poulsen J.G., Andersen P.N. & Elmegaard N. 1997. Skylark (*Alauda arvensis*) utilisation of micro-habitats in spring barley fields. Agr. Ecosyst. Environ. 62: 21–29.

Ottens H.J., Kuiper M.W., van Scharenburg C.W.M. & Koks B.J. 2013. Akkerrandebeheer niet de sleutel tot succes voor de Veldleeuwerik in Oost-Groningen. Limosa 86: 140–152.

Perkins A.J., Whittingham M.J., Morris A.J. & Bradbury R.B. 2002. Use of field margins by foraging yellowhammers *Emberiza citrinella*. Agr. Ecosyst. Environ. 93: 413–420.

Poulsen J.G. & Aebischer N.J. 1995. Quantitative comparison of two methods of assessing diet of nestling skylarks (*Alauda arvensis*). The Auk 112: 1070–1073.

Ralph C.P., Nagata S.E. & Ralph C.J. 1985. Analysis of droppings to describe diets of small birds. J. Field Ornithol. 56: 165–174.

Ramsay S.L. & Houston D.C. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. Ibis 145: 227–232.

Sage R.D. 1982. Wet and dry-weight estimates of insects and spiders based on length. Am. Midl. Nat. 108: 407–411.

Sillanpää S., Salminen J.-P. & Eeva T. 2010. Fluctuating asymmetry in great tit nestlings in relation to diet quality, calcium availability and pollution exposure. Sci. Total Environ. 408: 3303–3309.

Simpson S.J., Sibly R.M., Lee K.P., Behmer S.T. & Raubenheimer D. 2004. Optimal foraging when regulating intake of multiple nutrients. Anim. Behav. 68: 1299–1311.

Siriwardena G.M., Stevens D.K., Anderson G.Q.A., Vickery J.A., Calbrade N.A. & Dodd S. 2007. The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. J. Appl. Ecol. 44: 920–932.

Siriwardena G.M., Calbrade N.A. & Vickery J.A. 2008. Farmland birds and late winter food: does seed supply fail to meet

demand? Ibis 150: 585–595.
Skutch A.F. 1949. Do tropical birds raise as many young as they can nourish? Ibis 91: 430–455.
Smith B., Holland J., Jones N., Moreby S., Morris A.J. & Southway S. 2009. Enhancing invertebrate food resources for skylarks in cereal ecosystems: how useful are in-crop agri-environment scheme management options? J. Appl. Ecol. 46: 692–702.
Stoate C., Báldi A., Beja P., Boatman N.D., Herzon I., van Doorn A., de Snoo G.R., Rakosy L. & Ramwell C. 2009. Ecological impacts of early 21st century agricultural change in Europe – A review. J. Environ. Manage. 91: 22–46.
Taylor R.L., Maxwell B.D. & Boik R.J. 2006. Indirect effects of herbicides on bird food resources and beneficial arthropods. Agr. Ecosyst. Environ. 116: 157–164.
Tinbergen J.M. 1981. Foraging decisions in Starlings (*Sturnus vulgaris* L.). Ardea 69: 1–67.
Vickery J.A., Tallowin J.R., Feber R.E., Asteraki E.J., Atkinson P.W., Fuller R.J. & Brown V.K. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38: 647–664.
Vickery J., Carter N. & Fuller R.J. 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agr. Ecosyst. Environ. 89: 41–52.
Vickery J.A., Feber R.E. & Fuller R.J. 2009. Arable field margins managed for biodiversity conservation: a review of food resource provision for farmland birds. Agr. Ecosyst. Environ. 133: 1–13.
Waite T.A. & Campbell L.G. 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13: 439–442.
Weibel M. 1999. The diet of nestling skylarks *Alauda arvensis* in an intensively used arable landscape with wildflower strips. In: Effects of wildflower strips in an intensively used arable area on skylarks (*Alauda arvensis*). PhD thesis, Swiss Federal Institure of Technology, Zurich, pp. 62–80.
Westoby M. 1978. What are the biological bases of varied diets? Am. Nat. 112: 627–631.
Wiersma P., Ottens H.J., Kuiper M.W., Schlaich A.E., Klaassen R.H.G., Vlaanderen O., Postma M. & Koks B.J. 2014. Analyse effectiviteit van het akkervogelbeheer in Provincie Groningen. Rapport Stichting Werkgroep Grauwe Kiekendief, Scheemda.
Wilson J.D., Evans J., Browne S.J. & Jon R.K. 1997. Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in Southern England. J. Appl. Ecol. 34: 1462–1478.
Wilson J.D., Morris A.J., Arroyo B.E., Clark S.C. & Bradbury R.B. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agr. Ecosyst. Environ. 75: 13–30.

SAMENVATTING

In veel Europese landen zijn in het recente verleden akkerranden aangelegd om de voedselbeschikbaarheid voor vogels in het agrarische gebied te vergroten. Deze meerjarige, onbespoten randen worden dan ingezaaid met kruiden en grassen. Zij bevatten meer voedsel dan gangbare landbouwpercelen, waardoor ze voor veel vogelsoorten een geliefd foerageerhabitat zijn. Niet alleen de hoeveelheid voedsel is echter voor vogels belangrijk. Ook de diversiteit aan prooidieren kan de groei en gezondheid van nestjongen beïnvloeden. Om te onderzoeken of akkerranden effect hebben op de voedselsamenstelling van jonge Veldleeuweriken *Alauda arvensis* werden in 2011 en 2012 uitwerpselen verzameld in een gebied met intensieve landbouw in Oost-Groningen. Door middel van foerageerobservaties werd vastgesteld of de oudervogels gebruikmaakten van de ingezaaide akkerranden. Akkerranden bleken gedurende het grootste deel van het broedseizoen een grotere diversiteit aan ongewervelde dieren te bevatten dan de landbouwgewassen en gangbaar grasland. Coleoptera (kevers) vormden de belangrijkste prooigroep in het voedsel van zowel nestjongen als volwassen vogels. Het voedsel bestond verder vooral uit Diptera (tweevleugeligen), Lepidoptera (vlinders), Hymenoptera (vliesvleugeligen) en Araneae (spinnen). Nestjongen aten gemiddeld grotere prooien en een groter aandeel larven dan volwassen vogels. Bijna 75% van de nestjongen en volwassen vogels had plantaardig materiaal gegeten, wat er op zou kunnen wijzen dat er een tekort aan hoogwaardig, dierlijk voedsel was. Wanneer jongen werden gevoerd met voedsel uit de aangelegde akkerranden nam de diversiteit aan ongewervelde dieren in het voedsel zowel op orde- als familieniveau significant toe. De grotere prooidiversiteit in akkerranden zou, naast de grotere voedselbeschikbaarheid, mede de grotere aantrekkingskracht van akkerranden als foerageerhabitat voor akkervogels kunnen verklaren. Verder onderzoek moet uitwijzen of de grotere prooidiversiteit bij akkerranden ook daadwerkelijk een gunstige uitwerking heeft op de groei en gezondheid van de jonge vogels.

Corresponding editor: Theunis Piersma
Recieved 25 February 2014; accepted 13 July 2014

Appendices are available online
www.ardeajournal.nl/supplement/a102–161–171

APPENDIX

Table A1. Abundance and proportion of invertebrate taxa in the faeces of 66 Skylark broods aged 5–8 days, with estimated length and developmental stage.

Class Order Family	Abundance and proportion[a]			Mean length in mm (±SD)	% larvae and pupae
Arachnida	150 (9.3%)			6.5 (2.8)	
Acarina		1 (0.1%)		0.3 (–)	
Araneae		109 (6.8%)		7.0 (3.1)	
Linyphiidae			6 (0.7%)	2.2 (0.4)	
Lycosidae			36 (4.5%)	9.0 (1.40)	
Salticidae			5 (0.6%)	5.0 (0.0)	
Tetragnathidae			1 (0.1%)	–	
Opiliones		40 (2.5%)		5.4 (1.2)	
Phalangiidae			40 (5.0%)	5.4 (1.2)	
Diplopoda	2 (2.5%)			14.0 (8.5)	
Gastropoda	27 (1.7%)			4.6 (1.7)	
Stylommatophora		27 (1.7%)		4.6 (1.7)	
Insecta	1424 (88.0%)			11.1 (–)	
Coleoptera		705 (44%)		9.3 (3.4)	23
Byrrhidae			30 (3.7%)	7.3 (0.6)	
Cantharidae			16 (2.0%)	8.3 (2.7)	
Carabidae			322 (40.1%)	11.7 (3.0)	
Chrysomelidae			18 (2.2%)	5.2 (1.2)	
Coccinellidae			1 (0.1%)	5.1 (–)	
Curculionidae			37 (4.6%)	5.1 (1.2)	
Elateridae			74 (9.2%)	7.3 (1.0)	
Hydrophilidae			4 (0.5%)	4.3 (0.9)	
Scarabaeidae			9 (1.1%)	9.4 (3.4)	
Silphidae			2 (0.2%)	15.0 (0.0)	
Staphylinidae			6 (0.7%)	6.3 (1.9)	17
Diptera		250 (15.6%)		7.1 (4.1)	19
Scatophagidae			1 (0.1%)	7.0(–)	
Stratiomyidae			1 (0.1%)	11 (–)	
Syrphidae			4 (0.5%)	8.8 (1.5)	
Tipulidae			111 (13.8%)	15.7 (0.9)	
Hemiptera		39 (2.4%)		3.2 (2.0)	
Aphidoidea			21 (2.6%)	2.0 (0.0)	
Heteroptera			13 (1.6%)	6.5 (2.4)	
Auchenorrhyncha			4 (0.5%)	3.5 (1.3)	
Pentatomidae			1 (0.1%)	9.0 (–)	
Hymenoptera		200 (12.5%)		5.3 (1.6)	76
Cynipoidae			1 (0.1%)	1.0 (–)	
Formicidae			17 (2.1%)	4.7 (1.4)	
Ichneumonidae			1 (0.1%)	6.0 (–)	
Symphyta			163 (20.3%)	12.8 (6.9)	93
Lepidoptera		203 (12.6%)		18.8 (7.0)	64
Orthoptera		24 (1.5%)		12.2 (3.0)	
Acrididae			20 (2.5%)	12.9 (2.7)	
Neuroptera		1 (0.1%)		8.0 (–)	100
Chrysopidae			1 (0.1%)	8.0 (–)	100
Malacostraca	11 (0.7%)			12.0 (6.9)	
Isopoda		11 (0.7%)		10.2 (0.0)	
Clitellata (Oligochaeta)	4 (0.2%)			50.0 (0.0)	
Haplotaxida		1 (0.1%)		50.0 (0.0)	
Lumbricidae			1 (0.1%)	50.0 (0.0)	
Total nr identified	**1618**	**1611**	**968**		

[a]Proportion of group relative to the total number of specimens identified to that taxonomic level.

Table A2. Abundance and proportion of invertebrate and plant taxa in the faeces of nine adult Skylarks with estimated length and developmental stage.

Class Order Family Genus/species	Abundance and proportion[a]			Mean length in mm (±SD)	% larvae and pupae
Arachnida	7 (10.3%)			3.7 (2.4)	
Araneae		5 (7.4%)		3.2 (2.7)	
Linyphiidae			2 (3.7%)	2.0 (0)	
Lycosidae			1 (1.9%)	8.0 (–)	
Opiliones		2 (2.9%)		5.0 (0)	
Phalangiidae			2 (3.7%)	5.0 (0)	
Gastropoda	1 (1.5%)			3.0 (–)	
Stylommatophora		1 (1.5%)		3.0 (–)	
Insecta 60 (88.2%)			6.2 (3.6)		
Coleoptera		36 (52.9%)		5.7 (2.8)	
Byrrhidae			1 (1.9%)	7.5 (–)	
Carabidae			8 (14.8%)	8.1 (3.9)	
Chrysomelidae			3 (5.6%)	4.5 (0)	
Curculionidae			14 (25.9%)	4.4. (1.2)	
Elateridae			5 (9.3%)	6.4 (0.9)	
Hydrophilidae			2 (3.7%)	3.5 (0)	
Scarabaeidae			2 (3.7%)	9.0 (4.2)	
Diptera		9 (13.2%)		8.4 (5.7)	11
Tipulidae			3 (5.6%)	16.0 (0)	
Hemiptera		3 (4.4%)		4.7 (0.6)	
Heteroptera			3 (5.6%)	4.7 (0.6)	
Hymenoptera		10 (14.7%)		4.8 (2.3)	50
Cynipidae			2 (3.7%)	1.5 (0.7)	
Formicidae			1 (1.9%)	4.5 (–)	
Symphyta			5 (9.3%)	6.2 (1.8)	
Lepidoptera		2 (2.9%)		12.5 (3.5)	
Total nr identified	**68**	**68**	**54**		
Dicotyledonae	8 (32%)				
Asterales		2 (9.5%)			
Asteraceae			2 (9.5%)		
Caryophyllales		2 (9.5%)			
Polygonaceae			2 (9.5%)		
Monocotyledonae	17 (68%)				
Poales		17 (81%)			
Poaceae			17 (81%)		
Poa annua				5 (33%)	
Secale/Triticum var.				5 (33%)	
Setaria sp.				5 (33%)	
Total nr identified	**25**	**21**	**21**	**15**	

[a]Proportion of group relative to the total number of specimens identified to that taxonomic level.

Table A3. Abundance and proportion of plant taxa in the faeces of 66 skylark broods, aged 5–8 days.

Class Order Family Genus/species	Abundance and proportion[a]			
Bryophyta	4 (1.1%)			
Dicotyledonae	61 (17.2%)			
Asterales		6 (1.8%)		
Asteraceae			6 (1.8%)	
Taraxacum officinale				6 (2.0%)
Brassicales		18 (5.5%)		
Brassicaceae			18 (5.5%)	
Capsella pursa-pastoris				16 (5.4%)
Thlaspi arvense				1 (0.3%)
Caryophyllales		5 (1.5%)		
Caryophyllaceae			1 (0.3%)	
Stellaria media				1 (0.3%)
Polygonaceae			1 (0.3%)	
Geraniales		1 (0.3%)		
Geraniaceae			1 (0.3%)	
Geranium sp.				1 (0.3%)
Lamiales		9 (2.7%)		
Lamiaceae			7 (2.1%)	
Galeopsis sp.				1 (0.3%)
Lamium amplexicaule				6 (2.0%)
Plantaginaceae			2 (0.6%)	
Plantago sp.				2 (0.7%)
Malpighiales		2 (0.6%)		
Euphorbiaceae			1 (0.3%)	
Euphorbia sp.				1 (0.3%)
Violaceae			1 (0.3%)	
Viola sp.				1 (0.3%)
Monocotyledonae	289 (81.6%)			
Poales		288 (87.5%)		
Poaceae			288 (87.5%)	
Poa annua				1 (0.3%)
Secale/Triticum var.				256 (87.1%)
Setaria sp.				1 (0.3%)
Total nr identified	**354**	**329**	**329**	**294**

[a]Proportion of group relative to the total number of specimens identified to that taxonomic level.